
MINI REVIEW

ECOLOGICAL CONSEQUENCES OF CHEMICALLY
MEDIATED PREY PERCEPTION

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Abstract—To locate food, mobile consumers in aquatic habitats perceive and move towards sources of attractive chemicals. There has been much progress in understanding how consumers use chemicals to identify and locate prey despite the elusive identity of odor signals and the complex effects of turbulence on chemical dispersion. This review highlights how integrative studies on behavior, fluid physics, and chemical isolation can be fundamental in elucidating mechanisms that regulate species composition and distribution. We suggest three areas where further research may yield important ecological insights. First, although basic aspects of stimulatory molecules are known, our understanding of how consumers identify prey from a distance remains poor, and the lack of studies examining the influence of distance perception on food preference may result in inaccurate estimation of foraging behavior in the field. Second, the ability of many animals to find prey is greatest in unidirectional, low turbulence flow environments, although recent evidence indicates a trade-off in movement speed versus tracking ability in turbulent conditions. This suggests that predator foraging mode may affect competitive interactions among consumers, and that turbulence provides a hydrodynamic refuge in space or time, leading to particular associations between predator success, prey distributions, and flow. Third, studies have been biased towards examining predator tracking. Current data suggest a variety of mechanisms prey may use to disguise their presence and avoid predation; these mechanisms also may produce associations between prey

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distributions and flow environments. These examples of how chemical attraction may mediate interactions between consumers and their resources suggest that the ecology of chemically mediated prey perception may be as fundamental to the organization of aquatic communities as the ecology of chemical deterrence.

Key Words—Chemical attraction, chemosensation, community structure, flow, foraging, odor plumes, olfaction, orientation, predator-prey, turbulence.

INTRODUCTION

Over the last 15 years, investigating how natural metabolites mediate biotic interactions has provided valuable insight into the forces shaping the structure of marine communities. Chemical ecology is a vibrant field that helps explain why prey are rare, how animals should allocate energy in their defense, and the role of generalist versus specialist predators in regulating community structure (Hay, 1996). These issues have been studied largely through a focus on chemical defense, and studies of how chemical deterrents affect biotic interactions have become the type of investigation most closely identified with the field of chemical ecology in general. However, just as some chemicals deter consumers, others allow consumers to identify and locate prey from a distance. Although not as fully developed as the study of deterrents, the study of chemical attractants may be of equal importance in determining how biotic interactions affect populations and communities and is an area poised for exciting new developments.

Chemically mediated prey search and identification has been examined in a number of different organisms and in systems ranging from abyssal depths to shallow subtidal and intertidal communities. These studies have emphasized tracking behavior, the properties of sensory systems necessary for odor-guided navigation, or the characterization of attractant compounds. Only rarely have workers investigated the ecological implications of long-distance perception and location of prey in natural communities or realistic laboratory settings. We believe this reflects technical challenges in establishing basic features of chemically mediated attraction, rather than lack of appreciation for, or disinterest in, consequent ecological implications.

The molecular nature of chemical stimuli and the distribution of signals in nature determine how consumers are able to discern and locate prey. Thus, acquiring a basic understanding of the identity of attractant molecules and the physics of odor dispersal is necessary to evaluate the ecological implications of distance perception, but is technically challenging. First, consumers are more likely to use mixtures, perhaps of common compounds, rather than single cues to identify prey. In some cases, the difference between a highly attractive versus a less enticing mixture is simply the ratio of its components, rather than the presence or absence of a distinctive moiety (e.g., Carr and Derby, 1986a,b; Steullet and Derby, 1997).

Identifying attractant stimuli, therefore, is likely to be more difficult than determining the nature of a unique predator deterrent. Second, unlike most deterrent compounds, attractant compounds that mediate distance perception are released into the water. Consequently, extraction and identification of attractants must begin with aqueous solutions derived from intact prey and may be hindered by the considerable dilution of the stimulus. Third, because attractants are transported to animals by flow, it is also necessary to determine the properties of chemical signals in turbulent fluids. However, progress in understanding both the chemical nature of attractant compounds and the role of physical processes in structuring odor signals is now sufficient so that examining ecological implications of chemically mediated predation is feasible.

The purpose of this review is to summarize the progress in understanding chemically mediated prey search and to highlight the potential ecological implications of chemically mediated foraging for community organization. The current state of knowledge enables us only to hint at how prey identification and localization by waterborne cues may affect ecological patterns and processes. Yet, even these brief glimpses may help broaden the field of chemical ecology and move the study of chemical attractance beyond behavioral analysis and characterization of stimulus properties to an understanding of effects on population regulation and community structure. Given the availability of recent reviews on chemical plumes in relation to flow, navigational and guidance strategies, and the chemical nature of attractant compounds (Carr, 1988; Carr et al., 1996; Vickers, 2000; Weissburg, 2000; Zimmer-Faust and Butman, 2000), we focus this review more narrowly and address important issues that are still unsettled or ones where greater understanding may provide insights into basic ecological processes.

THE NATURE OF CHEMICAL ATTRACTANTS

Despite decades of investigation, the identity of waterborne attractants is still unclear, even for well characterized systems. This surprising fact has two main explanations. First, as noted above, chemical characterization of complex mixtures is technically challenging. Second, the goal of many early studies was to examine physiological properties of the chemosensory system of aquatic animals (e.g., Pearson and Olla, 1977; Carr, 1978; Carr and Derby, 1986a,b) that were poorly known at that time. Consequently, initial bioassays of attractant molecules tended to employ easily identifiable, common, and widely available constituents of animal (or occasionally plant) tissue such as amino acids, nucleotides, and simple sugars or organic acids. Although these chemicals are present in flesh, it is not always clear that they are released in sufficient quantities to mediate distance perception (see below), and they may primarily elicit feeding as opposed to orientation.

There is broad agreement that amino acids and other small molecules are highly stimulatory. Mixtures of 6–25 amino acids, sometimes with quaternary

ammonium compounds, nucleotides, and simple organic acids, have been extensively employed and usually are more effective than any single component (Carr, 1978, 1988; Zimmer-Faust and Case, 1982b; Carr and Derby, 1986a,b; Zimmer-Faust, 1989; Carr et al., 1996), although individual nucleotides can be highly attractive (Zimmer-Faust, 1993). For instance, Carr (1978) used a mixture of betaine and 18 amino acids to assay responses of the shrimp *Palaemonetes pugio*. Still, there is considerable debate regarding the significance of current observations for identifying attractant compounds. Although low-molecular-weight metabolites are clearly important feeding cues, the hypothesized primacy of these substances for orientation has not received a rigorous and comprehensive evaluation (Zimmer-Faust, 1989; Zimmer-Faust and Butman, 2000). Zimmer-Faust (1989) summarizes caveats and provides suggestions on ways to assay attractant compounds that are appropriate for examining distance perception.

Ecologically relevant experiments must present consumers with a flux of attractant molecules similar to that emanating from natural prey. Unrealistically intense chemical cues can stimulate chemosensors that normally mediate near-source search or feeding rather than distance search, because neurons in various appendages may be sensitive to the same suite of compounds but differ in their sensitivity to these chemicals (Caprio et al., 1993; Voigt and Atema, 1992; Weissburg and Derby, 1995). Consumers responding to abnormally elevated signals may not be displaying true distance tracking but, instead, behaviors that occur close to the source or reflexive motions involved in feeding and ingestion. Extracts of ground prey flesh almost certainly result in more intense signals and different mixtures of stimuli than consumers normally experience. Even prey soaks or body washes may produce unnatural stimulus intensities, particularly if prepared using multiple prey soaked in relatively small volumes for long time periods. Few studies have measured flux rates of potential attractant compounds released by living or dead prey as a way to scale flux rates of stimuli in experiments. Limited observations suggest considerable variance in the release of amino acids or ammonia waste products among different prey and differences in the quantity and identity of compounds released by injured, freshly dead, and live prey (Zimmer et al., 1999; Finelli et al., 2000). Mixtures of the 18 most abundant amino acids from bivalve or crustacean flesh released at natural flux rates attracted mud snails (*Ilyanassa obsoleta*) at rates to similar those of fresh carrion, but blue crabs remained disinterested in amino acid plumes mimicking the composition and flux from freshly injured clams (Zimmer et al., 1999; Finelli et al., 2000). Since flux rates in the two experiments differed substantially, the results do not necessarily indicate that crustaceans will not track amino acid plumes, only that injured bivalves do not release these metabolites in sufficient quantities. The concentration of amino acids released by live bivalve prey is less than that found in ambient seawater and below the limit of detection by HPLC, suggesting that amino acids are unlikely to attract consumers to bivalves under natural conditions (Zimmer et al., 1999). The

propensity of marine animals to absorb and not release amino acids (Wright and Manahan, 1989; Manahan, 1990) further suggests they may be generally inappropriate cues. Peptides mediate the predatory response of oyster drills at nanomolar levels (Rittschof, 1990), although the release rates from prey have not been determined. Lobsters appear to be attracted not to amino acids, but to unidentified high molecular weight compound(s) (Zimmer-Faust and Case, 1982a).

The search for a single compound, or even a class of compounds, that stimulates tracking in a particular species may be quixotic, particularly if composition and concentration is as variable across prey species as suggested by current studies (e.g., Zimmer et al., 1999; Finelli et al., 2000). Animals can detect a large number of compounds, and the combinatorial scheme used to identify chemical blends permits the recognition of a variety of mixtures (Derby and Atema, 1988; Sorensen and Caprio, 1997). Given this diversity in production and recognition, why should we expect animals to utilize only a limited range of potential information? It may be that certain compounds make poor signal molecules because they are naturally present at high concentrations with little correlation to prey availability or are not persistent over spatial or temporal scales that would facilitate tracking. A continued focus on identifying metabolites that serve as attractants under natural conditions and the environmental context in which they occur (e.g., flow, turbulence) will be necessary to resolve these issues. Future studies also are necessary to diversify the types of animals for which attractants have been successfully identified. Current data are overwhelmingly derived from predators or scavengers of carrion, with crustaceans being particularly well represented. Few studies have examined the orientation of herbivores to plant extracts or plant-conditioned water (but see Mann et al., 1984; Klinger and Lawrence, 1985; Rahman et al., 2000)

MECHANISMS OF ANIMAL NAVIGATION

Navigation to distant chemical sources often has been investigated in flumes using aqueous extracts of animal tissues (Moore and Atema, 1991; Moore and Grills, 1999) or occasionally, live prey (Weissburg and Zimmer-Faust, 1993, 1994). Perhaps the most important discovery from this work has been that odor signals available to large aquatic animals are affected significantly by turbulence (Zimmer-Faust et al., 1988; Moore and Atema, 1991; Weissburg and Zimmer-Faust, 1993). The resulting signal is complex, unpredictable, and highly variable in space and time (Figure 1), which constrains the strategies animals use to find distant chemical sources. Understanding how interactions between the signal source and environment affect the resultant plume characteristics, and how animals devise effective navigational strategies, can help establish the natural conditions where olfactory-mediated predation will be important.

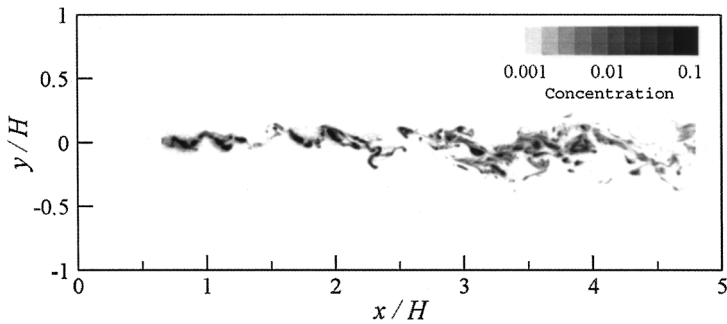


FIG. 1. Chemical concentration field of a turbulent odor plume generated in a laboratory flume. Image shows the chemical concentration field in a chemical plume measured by laser-induced fluorescence. The intensity of light emitted by a dye tracer is captured by a camera and converted to concentration, which is expressed as a proportion of the source concentration (inset). The y axis is the cross-stream distance and the x axis is the along-stream distance, each expressed relative to the water height, H (20 cm). Dye was released from a 3-mm-diam. nozzle located 2.5 cm above the bottom into a flow of 5 cm/sec. Flow is from left to right. Data and further details of this method may be found in Webster et al., (2002).

Crustaceans, fishes, gastropods, and echinoderms all orient to waterborne plumes of stimuli derived from animal flesh (Hamner and Hamner, 1977; Moore and Atema, 1991; Lapointe and Sainte-Marie, 1992; Weissburg and Zimmer-Faust, 1993; Montgomery et al., 1999; Weissburg, 2000). Herbivorous organisms, such as some Echinoidea, are thought to be opportunistic diners that find food through fortuitous random encounters, but this may reflect a lack of realistic tests. Several urchin species move towards palatable seaweeds (Mann et al., 1984; Tertsching, 1989) or selectively to seaweeds that differ in their value as food versus sheltering sites (Hay et al., 1986).

The most useful studies for understanding guidance mechanisms are those that take place in natural environments or in carefully controlled, hydrodynamically appropriate settings generated in flumes. Static tanks or Y mazes cannot accurately reproduce the fluid environment experienced by aquatic foragers and are of limited utility. Flumes have been popular due to the difficulty of visualizing animal behavior and monitoring flow in the field, but such facilities are constrained in the scales of turbulence they can generate. Consequently, we have a poor understanding of how large-scale flow features affect consumer foraging in nature. Limited observations suggest that some animals have difficulty following odor plumes with substantial cross-stream movements produced by large-scale turbulence (Lapointe and Sainte-Marie, 1992).

Crustaceans have been extensively studied in quantified or controlled flow conditions (Moore and Atema, 1991, Moore et al., 2000; Weissburg and

Zimmer-Faust, 1993, 1994; Finelli et al., 2000; Weissburg et al., 2002). Blue crabs, and probably most crustaceans, cannot sample long enough at a given location to estimate local average concentrations reliably due to their relatively rapid movement combined with high variability of turbulent chemical plumes (Webster and Weissburg, 2001; Weissburg et al., 2002). In fact, the difficulty of obtaining accurate mean estimates of many odor signal properties indicates they convey little information when sampled temporally, suggesting that using local averages to gauge upstream progress is unlikely to be successful (Webster and Weissburg, 2001; Weissburg et al., 2002). Blue crabs appear to utilize a combination of odor-triggered response to flow (rheotaxis) combined with spatial sensing of concentration fields (Zimmer-Faust et al., 1995; Webster and Weissburg, 2001; Weissburg et al., 2002). Together these two mechanisms allow animals to move generally upstream towards the source while maintaining contact with the odor plume. Odor-triggered rheotaxis appears common for many animals that search for prey in aquatic habitats (Weissburg, 2000).

Riverine or strongly tidal flows present relatively simple fluid environments where animals may rely commonly on rheotaxis because water movements are nominally unidirectional. Not only is flow information available to help guide navigation, but advection causes a net transport of odor, potentially resulting in a long-distance signal. In these simple flows, animals may follow plumes to baited traps located tens of meters away (Lapointe and Sainte-Marie, 1992; Skajaa et al., 1998), suggesting these regions may be unusually permissive of distant source localization, particularly if current velocities are slow and turbulence minimal (see below). However, animals in wave-driven oscillatory flows (Mead and Koehl, 2000), or in areas where bottom topography may produce complex currents (e.g., reefs) also are proficient foragers. A priori, we expect that the effective tracking distances in these habits will be reduced as compared to behavior in unidirectional flows, due both to the difference in physical transport and the absence of a reliable flow cue. Oscillatory flows limit the net movement of odor, whereas complex flows may create a more difficult signal to track because of both large-scale meander and the negative impact of small-scale turbulence (see below).

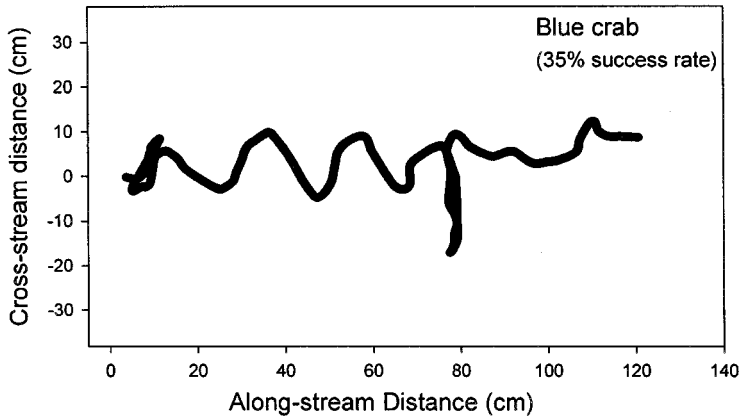
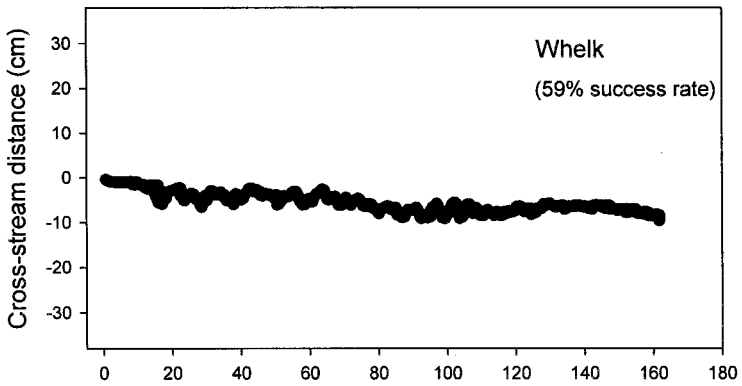
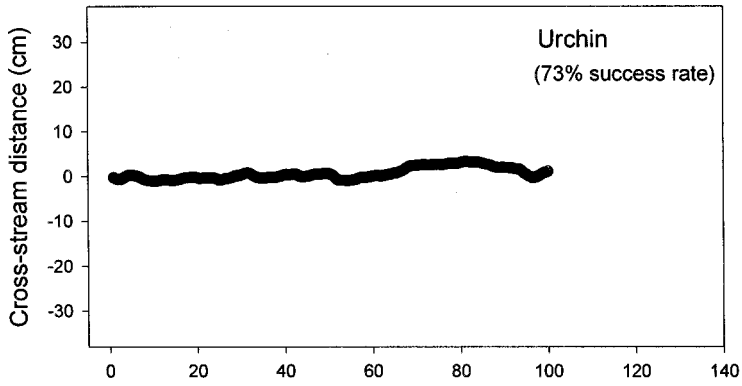
Animals inhabiting more complex flow environments may reduce their reliance on rheotaxis. Lobsters are thought to use predominantly chemical information during tracking, although firm tests are lacking and conclusions have been based on indirect evidence from studies in limited flow conditions or from behavior of animals with experimentally induced sensory deficits (Reeder and Ache, 1980; Devine and Atema, 1982; Moore and Atema, 1991). These observations provide evidence regarding the importance of chemical information but cannot exclude a rheotactic component. More direct tests are rare, but would include probing for upstream locomotion in response to brief chemical pulses or water velocities below which navigation is impaired (Weissburg and Zimmer-Faust, 1993; Mafra-Neto

and Cardé, 1994, 1998; Finelli et al., 2000), or examining whether animals follow flow streamlines. Flow provides potentially valuable information that could greatly enhance the efficiency of navigation, making it important to establish the conditions under which animals employ rheotaxis.

Animals may commonly use accessory cues such as flow or gravity to supplement information from chemical signals. An odor source that generates substantial turbulence in its wake or releases odor in the form of a vertical jet creates a plume that is initially elevated above the substrate and attaches to the bottom downstream of the source. Thus, consumers of substrate-bound food may interpret a sudden loss of signal to mean that they are close to the source. Foragers sometimes use the substrate as an accessory cue (thigmotaxis) and concentrate search efforts on the bottom following signal loss. Even capable swimmers may fail to find sources above the bottom when employing this strategy (Tamburri and Barry, 1999). Similarly, some pelagic animals tend to follow odors downward once they have detected a chemical signal (Hamner and Hamner, 1977), which might limit their ability to track mobile prey as opposed to passively sinking objects.

Turbulence disrupts odor plumes, renders individual filaments less detectable, and increases larger scale plume meander (Murlis, 1986; Moore et al., 1994; Weissburg et al., 2002). As expected, blue crabs show diminished search success and efficiency when challenged with more turbulent flows (Weissburg and Zimmer-Faust, 1993). Crayfish rarely seem inconvenienced by these conditions, and in fact, may search more effectively in moderate turbulence (Moore and Grills, 1999). The sensory basis for these behavioral differences in response to elevated turbulence remains unknown. For some animals, detrimental effects of turbulence may be a function of the relationship between animal sensory capabilities and length and time scales of odor features (Weissburg, 2000). Animals that move quickly through a plume perceive odor on a very coarse scale and have little choice but to respond to intense, instantaneous plume features. Sluggish predators may have the opportunity to sample more finely in time or space, resulting in an ability to estimate the local plume concentration that would be less affected by increased turbulence. Indeed, initial studies with whelks and echinoderms suggest that they maintain largely similar performance as turbulence is increased and have little apparent difficulty tracking odor in conditions where blue crabs are inefficient (Figure 2). In addition, blue crab search success is significantly lower at flow speeds

FIG. 2. Comparison of prey tracking in various aquatic animals. The figure shows typical paths of urchins (*Lytechinus variegatus*), whelks (*Busycon canaliculatum*), and blue crabs (*Callinectes sapidus*) tracking odor plumes in a laboratory flume. The odor source consisted of metabolites released from freshly dead, intact bivalves. All other conditions are the same as described in Figure 1. Shear velocity is approximately 3.1 mm/sec. Search success is given in parentheses.



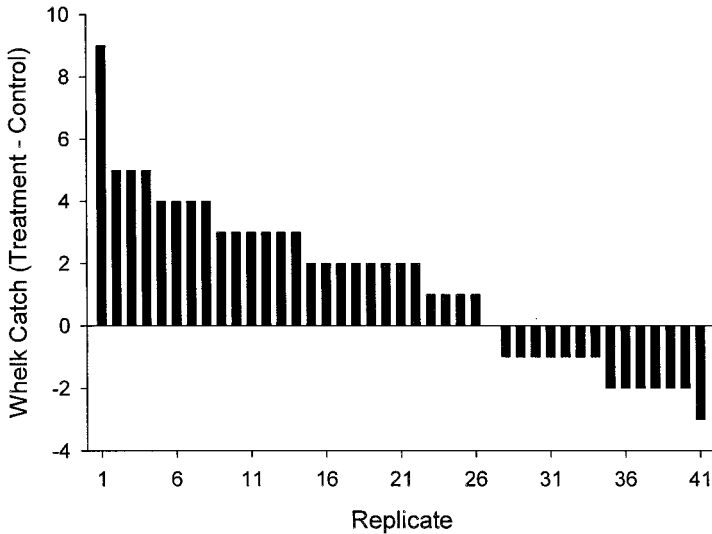


FIG. 3. Response of whelks to elevated turbulence in the field. Data show the difference between the numbers of whelks caught in traps modified to increase turbulence versus unmodified (control) traps. Traps generating increased turbulence caught an average of 1.4 more whelks than control traps and a pair-wise t-test indicates a significant effect of trap type on whelk catch ($t = 3.34$, $P < 0.001$, $N = 41$).

of 5 cm/sec than 1 cm/sec (Weissburg and Zimmer-Faust, 1996), whereas neither whelks (M. Ferner and M. Weissburg, unpublished data) nor urchins (D. Pisut and M. Weissburg, unpublished data) show decreased success across these speeds. In an initial study (M. Ferner and M. Weissburg, unpublished data), whelks were more attracted to baited traps that were modified to enhance turbulence when pairs of modified and unmodified traps were placed in similar flow environments (i.e., on opposite stream banks; Figure 3).

ECOLOGICAL IMPLICATIONS

Many aquatic organisms that hunt via olfaction can exert large effects on prey species, and sometimes, entire communities. Digging predators such as crustaceans or gastropods often control bivalve abundance (Virnstein, 1977; Micheli, 1997; Nakaoka, 2000), and their predatory activities cause local disturbances resulting in the death or emigration of non-target organisms (Pennings and Bertness, 2001). Such disruptions create considerable environmental heterogeneity that may be at least partially responsible for community patchiness. Urchins may aggregate in response to food, and dense urchin assemblages can denude large tracts of

vegetation (e.g., Estes et al., 1998; Rose et al., 1999). Given the current knowledge of chemically mediated foraging, it is opportune, perhaps essential, that we take steps to examine the ecological consequences of this process. Below we highlight a few avenues that may be particularly well suited in this regard.

Prey: Cueless or Clueless?

Until now, we have been fascinated by predator behavior, while prey have been relegated to the role of convenient stimulus sources. This short-sightedness may be understandable, but ignores the fact that predators evoke responses even from prey species often considered as having limited behavioral flexibility. As examples, when gastropods sense foraging crabs, they increase shell thickness and decrease foraging (Trussel, 1996). Mussels respond to consumers by thickening shells, increasing byssal attachment strength, and forming denser aggregations (Cote and Jelnikar, 1999; Leonard et al., 1999). Although prey cannot necessarily eliminate the expulsion of metabolites used as signals by predators, they may reduce the apparency of these emissions to make tracking more difficult for predators.

Given that some predators best track prey in conditions of smooth flow, regions of intense turbulence may represent a hydrodynamic refuge (Weissburg and Zimmer-Faust, 1993). This refuge may be spatial, resulting in the dispersal of prey into habitats with turbulent flow. It also may be temporal if prey actively liberate chemical cues during periods of high flow to render their signal undetectable. Some animals cannot feed unless they also expel waste plumes (e.g., bivalves). Prey attempting to hide their chemical signature consequently may suffer reduced growth as a nonlethal effect of minimizing their apparency to consumers. In fact, bivalves grow more slowly in the presence of predators, even when shielded from direct interactions (Nakaoka, 2000), suggesting alteration in the duration, and perhaps distribution, of feeding times.

Prey may have other means of disguising their presence beyond altering the timing of chemical release. Given the tendency of animals to search the ground for odor sources, animals may make themselves more difficult to locate if they expel plumes with sufficient vertical momentum so that chemical cues are transported far downstream before reattaching to the substrate. This strategy would be particularly effective when animals are in slow flows, since under these conditions the jet will travel farther from the substrate before its vertical momentum is lost (Moore et al., 1994). Animals that can capitalize on the ability to produce vertical jets may enjoy an advantage in slower flows relative to other potential prey.

Appropriate interindividual spacing also may reduce the risk of detection. Close neighbors may produce signals that interact (Monismith et al., 1990), increasing the cross-stream span of the plume as well as the flux of potential stimulants. Predators, therefore, may be more easily alerted to the presence of prey and find the signal easier to track than when they encounter plumes from a single individual.

Larger interindividual spacing may be particularly beneficial for prey that have a minimal impact on the surrounding flow (e.g., burrowing bivalves). Animals whose bodies generate substantial flow disturbances might actually benefit from aggregating more closely to enhance turbulence. If prey generate sufficient turbulence, their plume may disperse so quickly that it becomes difficult to detect even when prey density is high. These interactions may have implications for patterns of demography across regions of different odor-tracking permissiveness that have yet to be tested.

Significantly, prey often may use waterborne odors from predators to modify their behavior in response to immediate threats (Kats and Dill, 1998; Trussel, 1996). Habitats favorable for odor tracking may, therefore, increase both the ability to forage and to detect predators. Many animals, such as echinoderms, gastropods, or small crustaceans, are simultaneously both predators and prey. The ultimate consequences of enhanced odor detection are not predictable a priori but present a number of intriguing possibilities. For instance, foragers with more acute sensing of potential predators may be favored even in habitats where they may be more vulnerable to detection, whereas those less able to perceive predator odors may be restricted to more hydrodynamically marginal environments.

Competition and the Race for Food

The mounting evidence that olfactory foragers may differ in their skill at tracking signals in turbulent conditions suggests that individual predator species may be tuned for efficient foraging in given environments and that turbulence is a relevant dimension of the environment affecting the distribution and abundance of potential competitors. Even in the absence of strong competition, animals may gravitate towards conditions where they experience the greatest foraging success, suggesting that habitat choice, and consequently, the intensity of predation by particular species, may be affected by turbulence levels.

The partitioning of olfactory environments along a turbulence intensity axis may be particularly important for slow versus rapidly moving consumers, as these represent the end points of a spectrum of potential navigational strategies. In areas of low turbulence, a rapidly moving forager has the advantage, since plume conditions allow an animal responding to momentary bursts of intense odor to locate the source with speed and precision. A consumer employing this strategy reaches its goal before an animal using a time-consuming strategy dependent on local averaging. In more turbulent flows, the race for food is not necessarily to the swift, since local averaging may be the only effective tracking strategy where odor fields are dilute and bursts of high concentration are rare. As a result of the suitability of different navigational strategies across flow regimes, slow-moving time-averagers may be proficient at predation or scavenging in turbulent habitats, whereas more rapid crablike strategies should predominate where turbulence is

low. This hypothesis has yet to be examined. Since turbulence is affected by factors acting on regional (e.g., tidal amplitude) or local (e.g., bottom topography) scales (Wright, 1989; Mann and Lazier, 1991), the interaction between hydrodynamic environments and sensory strategies may produce differences in patterns of predation both between and within systems.

Predators that use different signal structures to locate prey would be expected not only to have distinct habitat preferences and predatory efficiencies even in similar environments, but perhaps preferences for different prey characteristics. By example, slow-moving consumers capable of computing local concentration can integrate in time to estimate flux, which for a given current speed is proportional to the product of metabolite concentration and release rate. Temporal integration is not necessary for rapidly moving animals that use perception of intense odor bursts to navigate. Flux is essentially meaningless for these consumers; instantaneous estimates of burst concentration provide the information used to find prey. Interestingly, crabs and whelks vary in size selectivity for their bivalve victims, with whelks tending to consume larger prey (Nakaoka, 2000). A number of potential explanations exist, but one possibility is that crabs and whelks do not use the same signal properties to guide navigation and, therefore, respond differently to prey of different sizes. Assuming larger prey have higher release rates, as opposed to releasing more concentrated stimuli, flux will increase, whereas properties of individual odor bursts may change little, if at all. Larger bivalve prey might, therefore, present a more attractive signal for whelks than smaller prey, which would be consistent with gastropods such as *Ilyanassa* that demonstrate increased aggregation to odor sources with greater fluxes (Zimmer et al., 1999). Crabs simply may be unable to discern prey size from a distance, and upon contact reject larger items in favor of smaller bivalves, which they can open more easily (Arnold, 1984). Alternatively, crabs may use some unknown odor or hydrodynamic feature, such as excurrent jet size or velocity, to select smaller prey. Chemically mediated strategies capable of producing differences in predation might serve to define, at least partially, functional guilds. Mobile aquatic predators often have been assigned to guilds based on foraging mode [e.g., burrowing, digging, sub-surface (Woodin, 1983) or stomach contents (Hines et al., 1990)]. These criteria may not be completely diagnostic when predators utilize different plume features in order to find their prey. Patterns of community regulation may be contingent on the degree to which its members are functionally redundant (members of the same guild; Strong, 1992), making accurate guild delineation necessary to thoroughly understand community dynamics.

Patterns of Preference

Many consumers in aquatic systems eat a variety of living prey (e.g., Hines et al., 1990), and some also may derive considerable nutrition from scavenging

(Britton and Morton, 1994). Factors that mediate patterns of prey choice have not been explored, particularly in realistic field settings. In the field, diet will be determined by the ability to detect an item from a distance, and once the prey has been contacted, by its palatability, degree of chemical or morphological defense, and nutritive value. In contrast, many feeding assays are conducted in small arenas where distance detection is minimized, so that postdiscovery factors are the primary arbiter of feeding decisions. This may confound accurate identification of consumer preference and result in unrealistic estimates of consumer impact on particular diet items. Nutritious, tasty, but undetectable food may be less prevalent in consumer diets than suggested by assays failing to account for distance perception.

Diet preferences also might be contingent on whether predators use differences in the quality (composition) of the odor signal or merely the quantity of stimulatory molecules, to identify and track their prey. The difference between these two scenarios is significant, since dining choices mediated by odorant composition reflect specialization on particular prey items, and specialists may exert different effects in communities than generalists. Understanding the basis of diet preferences, therefore, may help illuminate the role of given predators in aquatic communities. There is abundant evidence that aquatic predators possess the capability to identify chemical mixtures characteristic of particular food items and discriminate among them (Carr and Derby, 1986; Derby and Atema, 1988; Wight et al., 1990; Sorensen and Caprio, 1997). As noted above, it is unclear whether these stimulus mixtures are relevant to the task of source localization, as opposed to ingestion behavior. Chemical composition of amino acid solutions derived from injured prey has no significant impact on attractiveness of the snail *Ilyanassa* when presented at equal flux rates (Zimmer et al., 1999). One possibility is that scavengers use general and ubiquitous cues such as amino acids or nucleotides, whereas animals seeking live prey use more specific molecules. This supposition is consistent with the little evidence available regarding attractant compounds for scavengers and predators. Although *Ilyanassa* is primarily a deposit feeder, it must scavenge carrion for survival and reproduction (Curtis and Hurd, 1985). Juveniles of the predatory snail *Urosalpinx* feed exclusively on balanoid barnacles, which they find using a specific peptide cue (Rittschof, 1990).

CONCLUSIONS

The chemical ecology of deterrent compounds has provided insight into species interactions by successfully blending techniques from analytical chemistry, behavior, and ecology. The study of attractant compounds is poised to make important contributions, but in order to do so, must adopt a similar interdisciplinary perspective. The basic tools of chemical analysis, fluid dynamics, and behavior are now sufficiently advanced and, in some cases, have been combined in novel ways to examine odor tracking. The continuation of these efforts, particularly realistic

field experiments and in situ manipulations of chemical and fluid environments, has the potential to address many intriguing issues. With increased attention and effort, the ecology of attraction may become as important to understanding marine communities as the study of chemical deterrence.

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